6

Combat and Its Ritualization in Fiddler Crabs (Ocypodidae) With Special Reference to *Uca rapax* (Smith)[1]

JOCELYN CRANE

New York Zoological Society,
New York, New York 10460

(Text-figures 1-3; Plate I)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The station was founded in 1950 by the Zoological Society's Department of Tropical Research under the late Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see William Beebe, "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," *Zoologica,* 1952, Vol. 37, No. 13, pp. 157-184.]

CONTENTS

PAGE
I. Introduction 50
II. Historical Review 50
III. Materials. Methods, and Definitions 51
IV. Combat in *Uca rapax* 55
  A. Relevant Characteristics of Opponents 55
    1. Phase 55
    2. Relative size 55
    3. Claw of same or opposite side enlarged 56
  B. Behavior Components and Their Morphological Specializations 57
    1. Manus pushes 57
    2. Manus rubs 57
    3. Dactyl slides 57
    4. Heel-and-ridges 57
    5. Interlaces 58
    6. Taps 59
    7. Grips, flings, and upsets 59
  C. Associated Activities 60
    1. Withdrawals 60
    2. Mero-suborbital frication 61
    3. Downpushes 61
    4. Removal of burrow intruders 61
    5. Digging or prying out of opponent.. 61
    6. Afterlunges 61
  D. Categories 62
    1. Combats between an aggressive wanderer and a burrow holder..... 62
    2. Combats between two burrow holders 62
    3. Mutual combats 63
  E. Duration 63
  F. Postcombat Behavior 66
V. Combat in Species of *Uca* Other Than *U. rapax* 69
VI. Discussion 70
  A. Functions of Combat in *Uca*........ 70
  B. The Question of Adaptive Values of Combat Ritualization 72

---

[1] This study has been supported by the National Science Foundation (G-1316, G-21071, and GB-3600).

C. Derivation of Components 73
D. Comparisons with Ritualized Combat in Other Animals 73
E. Areas for Further Research 73
VII. Summary 74
VIII. References 75

I. INTRODUCTION

MALE fiddler crabs sometimes seize each other's large claws at the climax of a fight. Physical damage practically never occurs, although the stronger sometimes flings the weaker inches away or flips him altogether upside down. Almost all combats, however, stop short of a violent finish.

The work described in this contribution shows that most combats are so fully ritualized that the observer can detect no element of force. In these encounters the end activity is the rubbing or tapping of a correlated but different part of the opponent's claw. Morphological specializations include ridges, tubercles, and other structures with functions previously unknown.

At times the effective meeting of parts seems to be achieved through cooperative movements of the less-active crab. In the most elaborate combats the components are performed by each individual in turn, while his partner holds still.

Preliminary observations on ritualized combat in *Uca* were made in the Indo-Pacific (Crane, 1966). In some species the claws, partly engaged, vibrated back and forth with a clicking sound audible to the observer. Detailed descriptions were not secured in the field, although motion pictures recorded the pattern. In other forms, pits and tubercles apparently served as deterrents to forceful linkage of the chelipeds. These observations, made incidentally during a study of waving display, all showed the need for a concentrated study of combat.

The fieldwork described below was accordingly undertaken in Trinidad during 1966. A socially advanced neotropical species, *rapax*, was selected as the principal subject; comparative observations on other species have begun. The resulting contribution gives some basic information on the occurrence, organization, and results of combat and discusses its possible functions.

My thanks go to Pauline Thomas for Text-figures 1 and 3, to Julie C. Emsley for Text-figure 2, and to Kathleen Campbell for her aid in the laboratory and in reviewing film.

Headquarters for the study was the New York Zoological Society's William Beebe Tropical Research Station, Arima Valley, Trinidad, West Indies.

II. HISTORICAL REVIEW

The fighting proclivities of male fiddler crabs have long been familiar to naturalists and are even celebrated taxonomically in the species names *pugnax*, *pugilator*, and *bellator*. Compared with other conspicuous fiddler activities, however, combats are so uncommon, short, fast, and superficially similar that it is not entirely surprising that their patterned complexities have been overlooked. The infrequent reports have been only roughly descriptive and wholly unanalytical. Examples include Pearse (1912); Dembowski (1925); Verwey (1930); Crane (1958, 1966).

Intermale threat postures and movements in *Uca*, which certainly should be regarded as ritualized fighting, have been more fully reported, especially by Altevogt (1957), von Hagen (1962), and Schöne & Schöne (1963), in addition to the references just cited. This behavior is, however, arbitrarily excluded from the bounds of this contribution, where combat will be defined (p. 53) as any behavior between male *Uca* in which the claws of the chelipeds come into contact. For the same reason, references to waving display are excluded, although a great deal of waving is directed at other males and in many displays appears certainly to have developed in part from threat postures.

Intermale combat in other decapods occasionally has been reported but, again, only in general terms. It has been observed in other ocypodids, as follows: in *Dotilla*, by Tweedie (1954) and Altevogt (1957b); in *Heloecius* by Tweedie (1954); in both these genera as well as in *Scopimera*, *Macrophthalmus*, and *Ilyoplax* by Crane (unpubl.). Reese (1964), in a review of aggressive behavior in marine invertebrates, lists intermale ritualized combat as recorded in only three other genera of decapod crustaceans: the grapsid crab *Helice crassa*, observed by Beer (1959); another grapsid, *Pachygrapsus crassipes*, reported by Hiatt (1948), Bovbjerb (1960), and Schöne & Schöne (1963); and the goneplacid crab *Hemiplax hirtipes*, recorded by Beer (1959). Reese has not yet seen ritualized combat during his own investigations of pagurids although, as in a number of other decapods, intermale threat behavior and dominance relations occur.

Study of the acoustical behavior of *Uca* is now progressing (Salmon & Stout, 1962; Altevogt, 1962, 1964; von Hagen, 1962; Salmon, 1965; Crane, 1966), but the sounds of combat, which are occasionally audible to man, have yet to be examined. No tape recordings were made during the present study, although the above references form part of its background. The review by Guinot-Dumortier & Dumortier (1960) on the morphology of stridulation in crabs gives no examples where one crab is presumed to stridulate against part of another individual.

A survey of ritualization in animals—in the sense used first by Huxley (1914) and developed especially by Lorenz (1941), Baerends (1950), and Tinbergen (1952)—is included in Huxley *et al.* (1966). Ritualized combat is specifically discussed by Lorenz (1964, 1966a, 1966b).

III. MATERIALS, METHODS, AND DEFINITIONS

Unlike the casual observation of fiddler combat, its ethological study is slow and inconvenient. Not only does combat occur uncommonly, but its characteristics are often difficult both to determine and to record for a number of reasons.

First, the physical conditions under which combat is prevalent are stringent. At least in the tropics, combat seems frequent only near new and full moon, around the time of a diurnal low tide, and during the optimum hours of waving display for the species (Crane, 1958, p. 117). The correlation of prevalence of combat with the moon is, it seems at present, closer than that of waving; the closer connection may, however, be more apparent than real because of the rarity of combats compared with the frequency of waving and of threat postures. As with waving, combats are more frequent in sunshine than in cloudy weather, other conditions being equal.

A second difficulty lies in the fact that numerous combats are instigated by aggressive wanderers (*loc. cit.* p. 119; present contribution, p. 53). It is now clear that these examples are very often irregular. In working out the normal patterns, therefore, it is important both to see their beginnings and to observe the subsequent behavior of each crab long enough to determine whether an aggressive wanderer is one of the protagonists. This ideal procedure is often impossible in practice because combats usually start unpredictably and because afterward it is frequently difficult to keep watch on two crabs, one of which is moving rapidly away through a crowded population.

Third, details of activities involving the crucial inner surface of the manus are invisible in many encounters, even when the observer sits within inches of the combat.

Fourth, since most encounters start without warning and end after a few seconds, filming and acoustical recording are difficult.

There seem to be no short cuts to winning knowledge of the patterns. Until their occurrence and outlines were established in the field, it appeared unwise to depend on observations made in outdoor terraria and in the laboratory.

Preliminary attempts here and elsewhere to record the sounds of high-intensity fighting have not yet been successful. Both aerial and contact microphones have been used. Little time has so far been spent on this aspect of the work, however, since the basic activity patterns first had to be determined.

The data in this paper, therefore, are based wholly on fieldwork undertaken in Trinidad during the summer and fall of 1966 and on a review of motion pictures photographed on earlier trips to the Indo-Pacific and tropical America. The method of study was observation, note taking, scoring with and without binoculars, and photography with a 16-mm. Eastman Cine-special camera equipped with a 150-mm. telephoto lens. Combats were timed with a stopwatch and by mentally counting off seconds; for details see p. 53, under "Duration."

Most of the observations were made on *Uca rapax* (Smith), with comparative work on *U. cumulanta* Crane. These species were studied chiefly near the mouth of the Diego Martin River, west of Port-of-Spain. Active populations were selected in undisturbed areas.

All of the counts were made on a small plateau on the left bank of the river. Roughly circular, this area was about 15 feet in diameter. The terrain was typical for displaying populations of *rapax*—sandy mud that, although bare of vegetation, was adjacent to grasses and mangroves. The principal inhabitants were mature individuals of *rapax* and *cumulanta;* at optimum hours the great majority of males of both species displayed. *U. rapax* was more abundant on the top of the plateau, *cumulanta* on the damper, sloping sides, closer to the river and a tributary stream. The adjacent low ground supported flourishing populations of both species that were wholly without displaying individuals.

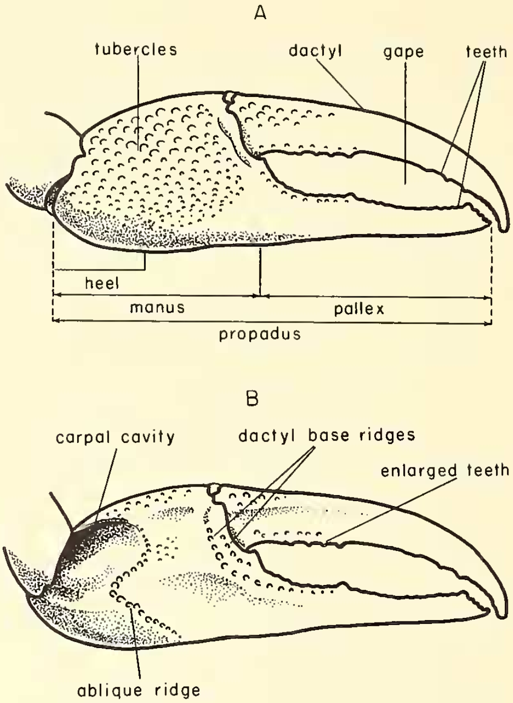
The portion of the plateau under observation was an arc of 120° with an average radius of 7 feet. About 75 to 100 *rapax* males displayed within this arc at any one moment during optimum display conditions. Three to five aggressive wanderers were usually active daily on the entire plateau, with one or two usually within the observation arc. To locate and count combats the arc was scanned without binoculars, by a single swing of the head averaging about 20 seconds; the swing was repeated at once if no combat was seen. When a combat or the strong threat of one was located, scanning ceased until all observational data possible had been noted from it, with or without binoculars.

The descriptions and counts in the following pages are based on 337 of these combats observed in sufficient detail to give information on one or more of the topics examined. Except where noted in the headings, therefore, the same combats were not necessarily included in all the tables or in the counts and percentages given in the text. The periods of observation totaled 30.5 hours under favorable lunar, tidal, and daylight conditions, distributed as follows during 1966: August 17-19 and 30-31; October 13-17; November 26-29. Excluded from these totals and dates are preliminary observations made before all the combat components were determined, along with their morphological specializations, their general sequence, and the existence of mutuality. Also excluded are combats occurring during an hour or more of observation under good conditions after every absence from the field, for example between the October and November sessions; for me this period of getting back into practice was an essential safeguard against false and incomplete observations. For similar reasons, no observations are counted that were incidentally made while photographing. Finally, combats are excluded that occurred during the first 15 minutes of every observation period; it appeared that this length of time, for this population of *rapax*, was more than enough for the crabs to become habituated to the observer's presence, so that their subsequent behavior was unaffected. (In disturbed populations and always when observing very large species a blind would be highly advisable for studies such as this.)

Tables I–VIII (pp. 55, 56, 60, and 64-67) show the number of observed examples of various kinds of combats and their components on which the accounts of *U. rapax* in the following pages are based.

Table IX (p. 69) lists species and numbers of combats filmed in previous years in which patterns were clear enough to give data now useful.

Text-figure 1 shows the location of the morphological parts of the male's large claw. A review of the terminology may be helpful to ethologists unfamiliar with crustaceans.



TEXT-FIG. 1. *Uca rapax*. Claw of major cheliped, to show location of structures used in combat. A, outer view; B, inner view.

The **claw** consists of the two terminal segments of the heterogonically enlarged first leg of the male. This entire appendage is termed the **major cheliped**; in this paper, since the minor cheliped is not mentioned, the adjective "major" will be omitted except in a few cases of possible ambiguity. The segments of the claw are (1) the **propodus,** consisting of the **manus** and the **pollex** ("fixed finger" of some authors), an extension of its lower part; and (2) the **dactyl** ("movable finger"), which is attached to the upper distal portion of the manus. The dactyl and pollex together form the **chela,** the grasping part of the entire claw. The word **heel** is used for the outer lower proximal portion of the manus, while **gape** denotes the space between dactyl and pollex. On the upper inner part of the manus is the **carpal cavity. Tubercles** of importance occur on the outer manus, on **ridges** of the inner manus, and close to the gape. Those of concern in the present study are: (1) on **outer manus:** enlarged tubercles, on either the upper or lower part of the manus, depending on the species; (2) on **inner manus (palm):** an oblique tuberculated ridge running from the proximal lower margin to the carpal cavity and sometimes continuing around the anterior margin of the cavity to the dorsal margin of the manus; (3) on **inner manus:** one or two tuberculated ridges, approximately vertical and roughly parallel to base of dactyl, the more proximal continuing ventrally in a curve around the base of the gape between dactyl and pollex and continuing for a way along the upper margin of the pollex; (4) on **pollex** and **dactyl;** submarginal tubercles and marginal **teeth** set along the gape, on the lower edge of the dactyl and upper of the pollex. Small tubercles or rugosities are often present on the upper proximal part of the dactyl.

Definitions of general terms are, for the purpose of this paper, as given below. Three considerations determined their selection. The first aim was to avoid misunderstanding in the use of words and phrases that are not always employed in the same way by all ethologists or that for this contribution needed limitation; an example is the word "combat." The second aim was to define terms that might be unfamiliar to workers who are not ethologists. Finally, specific combat activities and associated activities, a number of which are recorded for the first time in this paper, are briefly defined in the list; fuller descriptions, in context, follow on the indicated pages. To facilitate reference, the entire list of terms is given alphabetically rather than in any topical order.

Actor—In *Uca* combat, the individual at the moment performing the movements of a component.

Afterlunge—Feint by a burrow holder directed toward departing opponent. This activity is often associated with combat. (P. 61.)

Aggressive wanderer—A male *Uca* in the phase described below.

Aggressive wandering phase—The crab moves apparently at random through a population that includes displaying males, punctuates his passage with threats toward them, engages them in combat, makes superficial burrow explorations, and attempts unsuccessfully to mate. This phase is preceded by one of nonaggressive wandering. In *rapax* it is followed directly by the display phase, a predisplay territorial phase being apparently absent. Instead, the aggressive wanderer begins his waving display as soon as he occupies a particular burrow. For further details see below, p. 62.

Burrow holder—Equivalent, in *rapax*, to a crab in the display phase, always visually characterized by waving (see below). Because of differences found in other parts of the genus in the relationship of territoriality to display, the term "territory" and its derivatives are avoided in this paper, except in discussing the few combats that took place between burrows. In *rapax* the burrow itself is almost always the focus of combat, yet because of the frequent development of ritualization into a goal activity, it seems that strongly territorial terms such as "burrow defender" should not be used, even though some combats would make them wholly appropriate. Individuals, including females, that are not in display phase often occupy a burrow indefinitely; since they never engage in combat and never display, however, they are not concerned in this contribution; a serviceable term for them would be "burrow occupants."

Combat—A general term for any behavior between male *Uca* in which the claws of the chelipeds come into contact. Because of the usually high degree of ritualization, it might be preferable to substitute the word "encounter," thus avoiding the "loaded" words "combat" and "fight." Since the behavior discussed undoubtedly has an aggressive base, frequently shows overtly forceful components, and probably often includes pushing elements effectively masked by the ritualizations, it seems permissible to use all three terms. In this paper, therefore, "combat" is selected for general use; "encounter" appears occasionally in the discussion of fully ritualized combats; and "fight" is restricted to combats with overtly forceful components.

Component—An activity that is a characteristic part of combat and appears to the observer to be distinct from adjacent actions.

The most clear-cut examples are so distinct and so stereotyped that they may confidently be termed fixed action patterns, in the sense developed by Lorenz and Tinbergen and now often used in ethological studies. These examples are characterized not only by distinctive motor patterns but by juxtaposition of specialized morphological structures. In all of them overt force appears to be absent and they are here considered completely ritualized.

Other activities, however, are far less stereotyped and show considerable variability connected neither with intensity nor with transition to other combat actions. All of these, instead, often appear instantly adaptable to the changing circumstances of a fight. All show overt use of force since the chelipeds are used variously as a pushing, grasping, and lifting organ. These activities are regarded as unritualized. Any or all may need subdivision or other modification. Only further study with emphasis on comparative work within the genus can resolve the uncertainties.

Therefore it seems that the use of "fixed action pattern" would be at present a semantic disservice. The more general word "component" is adopted instead, in the same spirit shown by morphological taxonomists when they feel it premature to use a definite term such as "subgenus" and compromise on the noncommittal "group."

Dactyl slide—In *rapax* a ritualized component in which one crab rubs his dactyl teeth along the upper edge of his opponent's dactyl. (P. 57.)

Display—Here confined to a rhythmic motion of the major cheliped, species specific within the genus; movements of other appendages often accompany it. Used interchangeably with "waving" and "waving display."

Display phase—The phase characterized by waving, burrow holding, threat, combat, and courtship. In *rapax* it is preceded by the aggressive wandering phase.

Downpush—One crab is pushed down his own burrow by his opponent. An activity associated with combat. (P. 61.)

Duration—Timing of a combat from the moment at which the two chelipeds come into contact to their separation immediately preceding the departure of one of the opponents. Associated activities, ranging from preliminary threat behavior to afterlunges, were not timed, either as part of the combat proper or separately. Because of the difficulties of observing closely certain other constituents of each combat—especially its start, the phases of the opponents, their relative sizes, and their subsequent behavior—accurate timing with a stopwatch finally was discarded as a relatively expendable activity. Instead, counting seconds mentally was substituted, as in photography. Periodic checks with the stopwatch showed this system to be fully accurate within the broad limits of the two periods that turned out to be important to this study. During future fieldwork it will be feasible, now that the basic work has been completed, to concentrate adequately on duration, both of combats themselves and of associated activities. As will be seen from the discussion, such records now become imperative.

Encounter—Fully ritualized combat. (See also **combat.**)

Fight—Combat including forceful components. (See also **combat.**)

Fling—A variable, unritualized component at the close of a forceful ending. One opponent is pushed backward in a skid or is partly overturned. (P. 59.)

Forceful component—In low-intensity combat—manus pushes; in high-intensity combat—grips, flings, and upsets. All are highly variable and seem to be entirely unritualized, since the cheliped is used variously in pushing, grasping, and lifting.

Forceful end—Unritualized behavior at the end of a high-intensity fight, consisting of a grip by one opponent and sometimes followed by a fling or by the total upset of the other crab.

Grip—A forceful component consisting of the seizure by one opponent of the other's claw. (P. 59.)

Heel-and-ridge—A high-intensity ritualized component in which the actor places his dactyl outside the manus of his opponent while the pollex passes to the inner side, the palm, and rubs its oblique ridge. (P. 57.)

Heteroclawed combat—In one opponent the claw on the right side is enlarged, the other on the left.

High-intensity combat—Part of the claw of each opponent comes between the dactyl and pollex of the other. In forceful endings the claw tips may grip the opponent's claw; in fully ritualized encounters they do not do so. In *rapax* the available components consist of dactyl slides, heel-and-ridges, and interlaces; a low-intensity component, the manus rub, often initiates high-intensity combat.

Homoclawed combat—Both opponents have the claw of the same side, either right or left, enlarged.

Instigator—In combats between two burrow holders, the crab that approaches his future opponent; except for this approach, he does not necessarily ever become an actor. In combats between an aggressive wanderer and a burrow holder, the wanderer is always the instigator. Because of the usual high degree of ritualization, the words "aggressor" and "attacker" are not used.

Interlace—A ritualized component prevalent in heteroclawed combat. With the bases of both chelae almost in contact, proximal claw teeth on one crab rub against a distal manus ridge of the opponent. (P. 58.)

Left-clawed—Cheliped on left side enlarged.

Low-intensity combat—Contact is confined to the outer surfaces of the mani and chelae. In *rapax* the components consist of the forceful manus push and the ritualized manus rub. (P. 57.)

Manus push—See **Low-intensity combat.**

Manus rub—See **Low-intensity combat.**

Mero-suborbital frication—The rugosities on the upper merus of the cheliped are rubbed against the outer crenelations of the lower margin of the adjacent orbit. Behavior associated with combat. (P. 61.)

Mutual combat; mutual components—Both crabs perform one or more of the components, either in sequence or alternately. They can perform simultaneously only during manus rubs. (P. 63.)

Phase—A temporary condition of *Uca* characterized by one of a number of general behavior patterns. These have already been described (Crane, 1958). Of concern in this paper are the aggressive wandering and display phases, defined above. The term "phase" is retained here in preference to its possible alternate, "state," because the latter is often used in work with other animals for conditions controlled by long-term endocrine activity. At least in the tropics phases appear regularly to last only hours or days. The causes of phases remain uninvestigated.

Right-clawed—Cheliped of right side enlarged.

Ritualization—Any short definition or description of ritualization in animals must be inadequate. Furthermore, not all workers in ethology agree on the boundaries of ritualization or, rarely, even on the need for the concept. To me, however, much of the social behavior in *Uca* would be unintelligible without it. It is hoped that the following paragraphs may serve as a frame of reference for the present study of combat. Key contributions, classical and recent, on ritualization include Huxley (1914, p. 491; 1966, pp. 249–271), Lorenz (1941, 1964, 1966a, 1966b), Baerends (1950), Tinbergen (1952, 1953), Blest (1961), Hinde (1966, p. 432) and Thorpe (1966).

In animal behavior ritualization is an evolutionary process whereby social patterns develop partly through transformations of movements and structures that originally functioned during other activities. For example, a bird's courtship display movements may include recognizable traces of feeding and preening behavior. In the course of evolution both the motions and the associated morphological characteristics become simplified, exaggerated, or both. These changes often make a visual display, for instance, conspicuous, unambiguous, and distinct from that of related species. In short, they produce an effective signal in communication.

In other cases, ritualization serves to reduce intraspecific damage in combats between males. Here ceremonial encounters replace injury-producing use of weapons, while the advantages of aggression are maintained. The ritualized motions are often intention movements of actual fighting, more or less transformed and often, as in display, emphasized by the enhancement of associated structures. Also, as in display, parts of sequences from other contexts may be altered and included. Sometimes these combats are token tests of strength, and damage is avoided at the climax by stereotyped signals of posture and motions. Sometimes force seems wholly to be absent. Although ritualization in *Uca* combat obviously belongs in this general category, both its origins and its functions remain obscure, awaiting comparative study within the genus. They are briefly discussed, beginning on p. 72.

Ritualized combat—Encounters without forceful components.

Ritualized components—In *rapax* these include manus rubs, dactyl slides, heel-and-ridges, and interlaces. No pushing, grasping, or lifting motions are included.

Tapping—At the end of a ritualized component the teeth of the dactyl or the pollex or both tap against part of the opponent's dactyl or manus. (P. 59.)

Territorial phase—See **Burrow holder.**

Threat—Aggressive postures or motions confined, in male *Uca*, to individuals in the aggressive wandering, territorial, and display phases. Although threats usually precede combat, they occur far more often than combats. As in other animals they should be considered as classic examples of ritualized combat. Already described briefly and illustrated elsewhere (*ibid.*, 1958, p. 123; 1966, p. 464), they are arbitrarily excluded from this contribution through the selected definition of "combat." They will be further examined in a subsequent publication on the comparative ethology of combat behavior.

Upset—Unritualized, final component, where one crab is turned completely upside down. The rarest of all components. (P. 59.)

Wanderer—In the present paper used only for "aggressive wanderer," and then only where the latter term has already appeared in the same paragraph.

Wandering phase—In *Uca* a nonaggressive phase, characterized by lack of attachment to a particular burrow. It precedes the aggressive wandering phase (*ibid.*, 1958, p. 119). Not concerned in the present paper.

Waving; Waving display—See **Display.**

Withdrawal—Behavior associated with combat, where a burrow holder goes partway or entirely down his own hole. (P. 60.)

IV. COMBAT IN *Uca rapax*

A. *Relevant Characteristics of Opponents*

The pattern of a combat between *rapax* males depends largely on three factors: the phase of each individual; the relative size of the two crabs; and the location—whether on the right or left side—of the large claw of each.

1. Phase—Males engage in combat only when they are in either the aggressive wandering phase or the waving display phase. In the latter condition they are always burrow holders. Combats take place only between an aggressive wanderer and a burrow holder or between two burrow holders; encounters between two aggressive wanderers are unknown. When a wanderer elicits combat from a burrow holder irregular components are frequent and a ritualized encounter sometimes ends as a forceful fight. In contrast, combats between neighboring males are usually composed of highly regular, ritualized components and practically never end in force. These categories and their results will be described beginning on p. 62.

2. Relative size—The larger crab in all combats usually has the advantage. It is interesting, therefore, that in the majority of combats including an aggressive wanderer, the latter instigates combat with a burrow holder larger than he. See Table I.

TABLE I.

Uca rapax. RELATIVE SIZES OF OPPONENTS IN COMBATS WHERE INSTIGATOR WAS DETERMINED.
(Based on a total of 151 combats. Locality and dates as in Table II.)

Aggressive Wanderer vs. Burrow Holder		
Aggressive wanderer (always instigator) larger	22	
Aggressive wanderer smaller	66	
Aggressive wanderer & burrow holder about equal	6	
Total	94	94
Burrow Holder vs. Burrow Holder		
Instigator larger	36	
Instigator smaller	17	
Opponents about equal	4	
Total	57	57
Grand total		151

3. Claw of same or opposite side enlarged—In *rapax* right- and left-clawed individuals occurred in equal numbers in two population samples (unpubl.). In Maracaibo, Venezuela, the sample totaled 186; in the Trinidad study area, 252. Tables II and III show no tendency in combat for instigators to approach opponents having the same claw enlarged as their own rather than the claw on the opposite side. Therefore, homoclawed and heteroclawed combats are about equally likely to take place. Table III shows clearly that the frequency of several of the components described below is affected by this characteristic.

TABLE II.

Uca rapax. COMPOSITION OF 154 COMBATS OBSERVED AT COCORITE, TRINIDAD, OCTOBER 13-17 AND NOVEMBER 26-29, 1966.

(Note: Combats are listed only if observation is believed to have included the first component.)

Sequences of Components	*Combats Between an Aggressive Wanderer and a Burrow Holder*		*Combats Between Two Burrow Holders*		*Total*
	Homo-clawed	Hetero-clawed	Homo-clawed	Hetero-clawed	
Manus push only	1	..	1	1	3
Manus push + manus rub	..	..	2	2	4
Manus rub only	19	10	18	10	57
Manus rub + dactyl slide	1	13	3	6	23
Dactyl slide only	1	3	1	1	6
Manus rub + dactyl slide + heel-and-ridge	1	1*	1	..	3
Manus push + manus rub + heel-and-ridge	..	..	1	..	1
Manus rub + heel-and-ridge	9**†	4*	4	2	19
Dactyl slide + heel-and-ridge	1	..	1	1*	3
Heel-and-ridge only	5*†	..	5**	1	11
Manus rub + interlace	..	5†	..	..	5
Heel-and-ridge + interlace	..	4	..	..	4
Interlace only	..	2†	..	2	4
Manus rub + heel-and-ridge + interlace	1	..	..	..	1
Dactyl slide + heel-and-ridge + interlace	..	1†	..	..	1
Manus rub + dactyl slide + heel-and-ridge + interlace	..	3†	..	1	4
Manus rub + dactyl slide + interlace	..	2	..	1	3
Dactyl slide + interlace	1	1	..	..	2
Total	40	49	37	28	154

* 1 heel-and-ridge component not followed by tapping.
** 2 heel-and-ridge components not followed by tapping.
† 1 combat with forceful ending included.

TABLE III.

Uca rapax. RELATIVE FREQUENCY OF COMPONENTS IN 154 COMBATS.
(From data in Table II.)

Component	*Frequency (%)*	
	In 77 homoclawed combats	In 77 heteroclawed combats
Manus push	6	4
Manus rub	78	77
Dactyl slide	14	44
Heel-and-ridge	38	23
Interlace	3	29

B. Behavior Components and Their Morphological Specializations (Tables II and III)

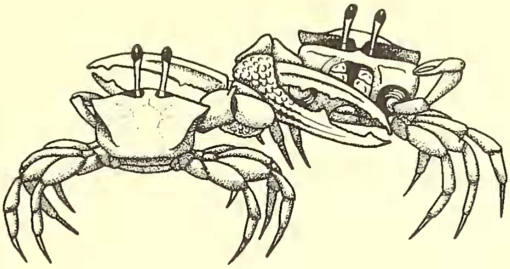
All combats are based on seven components. These are described below, in the order of their usual occurrence. Component 1 or 2 or both may form the entire combat; usually 2 precedes one or more additional elements. Components 1 and 2 are regarded as low-intensity components, and 3 through 6 comprise the highly ritualized, high-intensity components. The infrequent forceful grips and upsets are grouped under Component 7.

As shown in Table II, all the components never occur in a single combat. The sequence given below is altogether characteristic, but reversals of order among high-intensity components occasionally take place, particularly in long mutual combats. These reversals may or may not be followed by repetitions of previously performed components. The combat pattern, therefore, is not rigidly constructed of a fixed sequence of interdependent components. The omissions and irregularities are such that it does not seem wise to stylize the data so far assembled into a diagram of a "typical" combat sequence, or even into any kind of flow diagram. Instead, it is felt that tables present the complexities of the subject in a more realistic manner.

1. Manus pushes—The chelipeds are held flexed, the chelae partly open through slight lifting of the dactyls. Meanwhile the lower, smoother halves of the mani are pushed against each other. It often seems impossible to decide whether or not a manus push includes a rub component or vice versa, and the totals given in the tables are approximate.

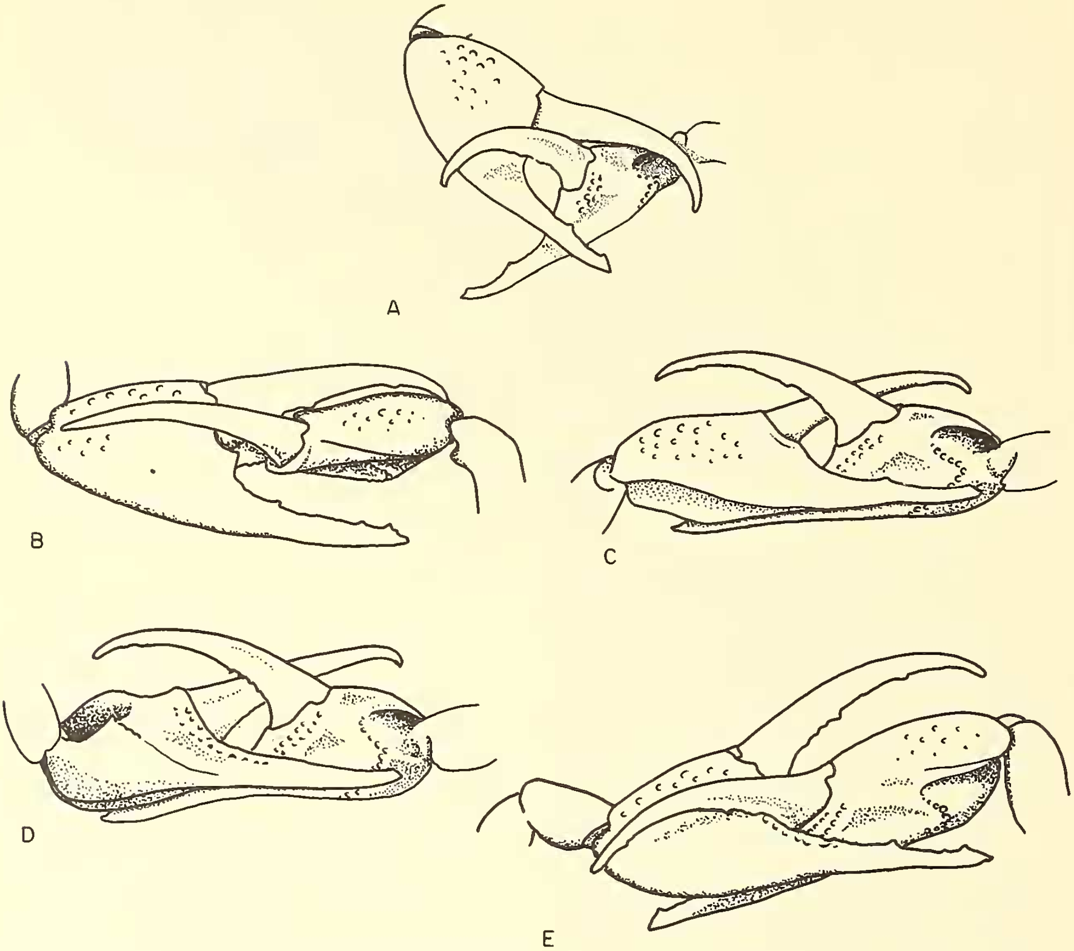
2. Manus rubs—The same surfaces as in the manus push are rubbed back and forth, longitudinally, against each other. In *rapax* and related species the surfaces in contact are smooth, rather than coarsely tuberculated as in some other sections of the genus (Text-fig. 2). It is possible that the rubbing over the smooth surface facilitates the attainment of high-intensity components. At these times the manus rub continues past the bases of the gapes until the chelae are in contact externally and are free to proceed to one or more of the following positions.

3. Dactyl slides (Text-fig. 3A)—With the chelae of both crabs partly open, the dactyl of one moves on top of that of the opponent, at about middle of its length, more or less at right angles, while the pollex passes within the gape. The approach may be from either the inner or the outer side of the claw. Both chelae are by then widely opened and the pollex does not touch the opponent's fingers. Gentle maneuvering for this position may continue for several seconds. Once it is achieved, the rounded teeth of the actor's dactyl slide longitudinally back and forth along the smooth middle portion of the upper edge of the opponent's dactyl. No force seems to be used by either crab and no attempt is made to use the claws as pincers, all four tips being at all times free in the air. Except for the sliding motion both crabs remain almost motionless. An infrequent climax is the vibratory tapping of the uppermost dactyl against the one held quietly beneath it. In this species the vibration is performed only by the crab with the dactyl on top. Afterward the two crabs break suddenly apart. When tapping does not occur, the encounter either breaks off after at most several seconds of slide or, infrequently, passes into Component 4 or 5 below. Dactyl slides occur more often in heteroclawed than in homoclawed combat.



Text-fig. 2. Low-intensity combat in *Uca*. Semi-diagrammatic view of position assumed by many species throughout the genus during manus pushing and rubbing. During homoclawed combat, as above, the manus of each opponent sometimes lies against the opponent's pollex. In heteroclawed examples the claws are usually lined up parallel, from manus heel to chelae tips. The dorsal margins of the mani are sometimes, as in the figure, at unequal heights, sometimes at the same level. See text, p. 57.

4. Heel-and-ridges (Text-figs. 3B, 3C; Pl. I, Figs. 1, 2.)—In *rapax* and many other species the dactyl, longer than the pollex, curves downward beyond it. This characteristic proves to be of definite use in heel-and-ridging, where the dactyl arches around the curving heel outside the manus of the opponent. On its way toward the heel, the dactyl tip appears to feel its way, using as a guide the outer crease along the base of the dorsal marginal ridge. Afterward, upon reaching the proximal part of the manus, the dactyl tip does not touch the heel except during the climax to be described. Meanwhile the pollex, shorter than the dactyl and virtually straight, comes into contact with the oblique tubercu-



Text-fig. 3. High-intensity combat in *Uca rapax*. A, dactyl slide; B and C, heel-and-ridge with tapping in homoclawed encounter; D and E, interlace in two forms of encounter. In B the crab on the left is the actor, his dactyl tip touching his opponent's heel; in C the same actor's pollex on a reverse stroke is hitting the opponent's oblique ridge, his dactyl tip being now separated from the heel; the same pollex position is used during the rubbing of the oblique ridge during the earlier part of the component. The interlace shown in D illustrates the more usual, heteroclawed form of this component; the right-clawed crab on the right is the actor, getting into position to bring dactyl teeth against opponent's ridge along inner base of dactyl; see also Pl. I, Figs. 3 and 4. E shows the interlace in its less common form, in homoclawed combat; the crab on the right is the actor, rubbing basal teeth of dactyl against basal teeth and outer tubercles of opponent's pollex. See text, p. 57 ff.

lated ridge of the inner manus. The pollex teeth, in the seven examples where an adequate view or film was secured, rub up and down along the oblique ridge. At the climax, however, the actor taps the ridge rapidly three or four times with his pollex; on opposite strokes, when the pollex is away from the ridge, the teeth near the dactyl tip come into contact with the manus heel. At highest intensity the tapping is faster and of smaller amplitude; the effect is vibratory (p. 59). When crabs are not closely matched in size, the parts coincide poorly and it is the acting crab—not necessarily by now the original instigator—that performs the tapping. No attempt at seizing and gripping has ever been detected when the claws are in the heel-and-ridge position. A heel-and-ridge, with or without tapping, may be preceded by a manus rub or infrequently by a dactyl slide. Occasionally in mutual, heteroclawed combat a heel-and-ridge is followed by or alternates with an interlace.

5. *Interlaces* (Text-figs. 3D, 3E; Pl. I, Figs. 3, 4.)—In this component the fingers of each claw overlap the opponent's manus, so that the

bases of the gapes are almost or wholly in contact. The sequence is characteristic of heteroclawed combats although not confined to them. Typically the position is assumed by the crab that has its dactyl against the inner side of the opponent's manus rather than against the outer side, which is the position for a heel-and-ridge. In a fully developed interlace the chela of each crab is wide open through high elevation of the dactyl; the tips of both pollex and dactyl are wholly free from contact with any part of the opponent. In this position the most proximal teeth of the pollex come into contact with one or both of the tuberculated ridges paralleling the base of the opponent's dactyl and rub up and down along their course. At highest intensity the rub follows along the longer, less-variable subdistal ridge that continues from the dactyl base down around the base of the gape and out along the proximal, upper, inner portion of the pollex.

The climax usually consists of frication by the pollex teeth as just described, whereupon the encounter ends. This component may culminate in serial taps similar to those following a normal heel-and-ridge component but made, instead, by the basal gape teeth against the subdistal ridge of the manus in the interlace position. While a tapping finale is the normal end of a fully developed heel-and-ridge component, it is uncommon after an interlace and, as when it follows a dactyl slide, cannot be regarded as typical (p. 57).

An interlace is usually preceded by a manus rub and less often by a dactyl slide. It also occurs in mutual heteroclawed encounters when one opponent, with the dactyl against the inner side of the other's manus, performs the interlace. Usually it is the temporarily more active crab, in passing from a low-intensity manus rub to high-intensity, that assumes the heel-and-ridge position, with the dactyl outside the manus; hence the second crab arrives automatically in a position appropriate for the interlace.

6. *Taps*—As already described, tapping occurs most frequently at the end of a heel-and-ridge component. Sometimes it is preceded by an interlace or dactyl slide; rarely by a manus rub. Always it consists of the rapid tapping of the dactyl or, in most heel-and-ridge sequences, of the dactyl and pollex alternately, against a particular part of the opponent's claw. Rather slow tapping of wide amplitude is performed both by aggressive wanderers and by burrow holders. Rapid taps of narrow amplitude are performed only by a burrow holder, usually at the end of an encounter beside his own hole. The several examples recorded on motion picture film appear as blurs on frames exposed at 1/48 second. After tapping, a combat often breaks off abruptly.

7. *Grips, flings, and upsets*—In contrast to Components 2 through 6, the occasional forceful end of a combat is composed of irregular elements that appear to be largely or wholly unritualized. They may be grouped under grips, flings, and upsets—descriptive terms for actions that merge into one another.

A grip occasionally follows an unsuccessful attempt by an aggressive wanderer to get into the heel-and-ridge position; the fingers then slip beyond the normal position and firmly seize the base of the manus with one finger hooked into the carpal cavity; even the carpus itself may be grasped. Sometimes grips occur when two crabs are grossly mismatched in size; then the larger may seize the entire manus of the smaller crosswise between his fingers. More often the forceful component consists only of a longitudinal grip, with perhaps an undetected push, the actor then opening his fingers. Almost always the crabs then separate.

The term "fling" here includes those actions, always starting with a grip, that result in a skid or partial upset of the opponent. The momentum of the actor's pushing grip carries the released crab sliding backward, or he is thrust off balance with some of his ambulatories off the ground. "Upset" is confined to actions resulting in the complete overturn of the opponent onto his carapace, with all of his ambulatories in the air.

Both the occurrence and the progress of these forceful endings have so far proved to be unpredictable. The following figures are relevant. In 180 combats in which the endings were adequately observed, 15 (8.3%) ended forcefully (6 of these are included in the group of 154 combats analyzed in Table II and are so indicated). In 14 fights the opponents were an aggressive wanderer and a burrow holder; the wanderer was larger than the burrow holder in 7 combats, smaller in 6, while his identity was uncertain in 1; homoclawed and heteroclawed combats were equally divided. In 6 fights the forceful component consisted of a grip only, 5 others ended in flings, and only 3 in total upsets. The burrow holder was the actor both during the preceding ritualized component and in the grip and subsequent action in 7 combats, the aggressive wanderer in 2, 1 of them resulting in the eviction of the burrow holder; in 2 fights both ritualized and force components were mutual, 1 of them resulting in the second observed eviction of a burrow holder; in 1 fight the action consisted wholly in the eviction of an aggressive wanderer that had slipped in while the burrow holder was engaged with a neighbor. The ritualized components immediately preceding forceful endings were interlaces in 7 fights and well-developed heel-and-ridges with taps in 3; antecedents to the grip in the remaining examples were irregular or improperly observed. Finally, 5 fights were followed by reduced aggressiveness of the wanderer and 2 by the dispossession of a burrow holder by a wanderer.

The single forceful ending to a combat between burrow holders was very short; the slightly smaller instigator lightly seized the opponent's entire palm then released it and went home; both crabs promptly resumed waving.

In brief, about 1 in 12 combats had a forceful ending, usually consisting only of a brief grasp by one crab of the other's manus; 14 out of 15 fights were between an aggressive wanderer and a burrow holder; in most the burrow holder was the active crab at the end of the fight, seizing the wanderer and administering the final push, fling, or upset. Forceful components preceded reductions in the wanderer's aggressiveness in 5 combats and preceded the taking over of his opponent's burrow in 2. These changes in behavior will be further discussed beginning on p. 66 and are included in Table VIII.

C. *Associated Activities*

1. Withdrawals—Of the 154 combats observed most completely, one quarter included some degree of withdrawal by the noninstigating crab into his own burrow. These withdrawals are subdivided in Table IV, but the degrees indicated form unsatisfactory comparison material.

As shown in Table I, in the majority of combats between aggressive wanderers and burrow holders, the wanderer, always the instigator, is usually smaller than the burrow holder. Conversely, in encounters between burrow holders, the instigator, which usually starts the combat at the mouth of his opponent's burrow, is most often the larger crab.

Withdrawal of an approached crab, it seems, would be a more likely action by a crab smaller than his opponent than by one larger than the instigator. It would be expected, therefore, that in combats involving wanderers there would be little withdrawal underground, since most wanderers are smaller than the burrow holders they approach. In contrast it would seem predictable that since burrow holders are usually engaged by larger burrow-holding neighbors, withdrawals among the first would be more numerous.

In the material at hand as shown in Table IV such differences are not apparent. Withdrawals of burrow holders in combat with aggressive wanderers are more numerous than those between burrow holders. A principal reason is that the figures for partial withdrawals in Column 3 are misleading elements in the totals. They are misleading because partial withdrawals are not often functional withdrawals from combat. In these cases the burrow holder instead clearly uses the upper part of his burrow as a firm foothold for the prosecution of the encounter. In the samples given in the table, as well as in a

TABLE IV.

Uca rapax. COMBATS INCLUDING WITHDRAWAL OF THE NONINSTIGATING CRAB INTO HIS OWN BURROW.

(Based on a total of 154 combats. Locality, dates, material as in Table II, p. 56.)

Key: AW........ Aggressive wanderer
BH .... Burrow holder

1 *Type of Combat*	2 *Relative Size of Crabs*	3 *Degree of Withdrawal of Noninstigator* Major side appendages above ground	4 Claw alone left above ground Manus and chela flat on surface	5 Chela tip vertical in air	6 Crab wholly underground	*Total*
AW & BH	AW larger	3	3	1	5	12
	AW smaller	6	2	0	2	10
BH & BH	Instigator larger	5	0	3	7	15
	Instigator smaller	1	0	0	0	1
Total		15	5	4	14	38

number of other combats witnessed too incompletely to be included, I have seen these half-withdrawn burrow holders engage most effectively in all classes of combat. These engagements ranged from the most unritualized and violent upset of a wanderer to the delicate mutual frications of well-matched neighbors.

Column 4 in the table is almost equally unsatisfactory, giving no indications of the prevalence of examples where the manus and chela are laid flat on the surface. Almost always this behavior is shown by a burrow holder that does not engage at all in combat with an approaching aggressive wanderer but simply withdraws below ground before the wanderer can touch him, leaving the manus and chela in sight. Hence the behavior properly belongs under the general heading of threat rather than of combat as defined here, and so is beyond the scope of this paper. The wanderer may or may not make prying motions at the claw with his own chela or ambulatories, or may even stamp on it before passing on. Only twice have I seen this type of withdrawal during an encounter where both opponents may have been burrow holders; these are not included in the table since they occurred in combats where the phase of the instigator was not certainly determined.

These flat-clawed partial withdrawals from aggressive wanderers have been observed often in other species. In all, they seem to occur principally in crowded populations. Unfortunately counts and distance measurements have not even been begun.

Where the chela tip appears vertically above ground (Column 5), it seems probable that the projecting tip represents a different degree of withdrawal mood in the retired crab.

Withdrawal wholly underground (Column 6) almost always occurs when the crab's opponent, whether aggressive wanderer or instigating neighbor, is larger than he.

2. *Mero-suborbital frication*—In two of the encounters between burrow holders in which the noninstigator withdrew, his opponent reached briefly down into the burrow with his small claw. The merus of the major cheliped meanwhile rubbed three to four times against the enlarged outer crenelations on the lower margin of his orbit. I have also twice seen the motion performed by *rapax* when wanderers reached down occupied burrows with the legs of the side opposite the large claw and, in the Indo-Pacific, by *U. vocans* (Herbst) in threat behavior when both opponents were on the surface.

3. *Downpushes* —In four examples observed in detail a crab actively pushed his opponent down the latter's own burrow. Three of the combats were between burrow holders, the actor using the low-intensity manus push. In one of these the instigator was the smaller crab; the larger pushed him back to his own burrow, alternating manus pushes with manus rubs. The fourth downpush marked the end of a meeting between an aggressive wanderer and a burrow holder; the downpush was the only noteworthy part of the brief combat, which included a manus rub and an irregular interlace. In this fight the downpush was delivered by a final grip.

4. *Removal of burrow intruders*—Three times when a burrow holder returned to his hole after a combat nearby a third crab was in possession. On two of these occasions the returning crab dug the intruder out. On the third, the burrow holder, which was much the larger crab, thrust his major cheliped down the hole and flipped the smaller out; the action was too rapid for me to note details. In no case was the incident followed by any of the components of regular combat.

5. *Digging or prying out of opponent*—Only once was a digging or prying out motion observed during a regular combat. Here an aggressive wanderer had engaged a slightly larger burrow holder. At the end of an encounter composed of a manus rub, dactyl slide, and heel-and-ridge without tap, the burrow holder slid slowly down his hole. The wanderer disengaged, tried briefly to dig the other out with his major cheliped, and then departed.

6. *Afterlunges*—The term "afterlunge" is given here to an action frequently associated with combat, although the same or very similar behavior sometimes occurs in purely threat situations. With the cheliped more or less flexed, the crab lunges toward the opponent—either potential or recent. When associated with combat, an afterlunge always follows the encounter, sometimes so closely that perhaps it should then be considered a component. Such distinctions between afterlunges, however, would be too blurred to be practical.

The afterlunge was counted in 54, or almost half, of the 112 combats of all kinds in which its presence or absence was noted. It was almost always performed by the larger crab, and, except in boundary encounters, occurred at the mouth of his own burrow. Usually it followed a combat between an aggressive wanderer and a larger burrow holder—that is, the most frequent kind of encounter; 65% of all afterlunges followed such an engagement. Afterlunges were also common after boundary combats between burrow holders; one occurred, always performed by a single crab, in 9 out of the 12 fully observed boundary encounters; in 7 of these examples the larger crab was the actor.

Particularly in combats including an aggressive wanderer, the burrow holder sometimes lunged just as the two crabs were separating and through this movement may even have brought about the wanderer's departure; these examples added an element of virtual force to an otherwise wholly ritualized and often mutual encounter. More often the burrow holder did not lunge until the wanderer, or instigating neighbor, was already at a distance. Once a small, instigating, burrow holder atypically lunged toward his former opponent after his return to his own burrow. Finally, after one of two forceful burrow seizures, the former aggressive wanderer waved and then lunged toward the dispossessed crab, which was circling about in the low posture characteristic of nonaggressive and nondisplaying *Uca*. This unusual example was the only combat seen where an afterlunge followed a forceful ending.

D. Categories

The preceding accounts of behavior components have mentioned two general classes ot combats, those between an aggressive wanderer and a burrow holder and those between two burrow holders. The characteristics of each will now be considered as a basis for a review of combat results. Mutual combat occurs in both categories but will be examined more closely under subheading 3 below.

1. Combats between an aggressive wanderer and a burrow holder—These combats are notable for their irregularity, for the prevalence of forceful grips, and for the frequent withdrawal of a vigorous burrow holder from an encounter. In first determining the combat repertory of any species of *Uca*, in fact, it is misleading to concentrate on combats involving aggressive wanderers. Such descriptions might easily be as inaccurate as reports on the nest-building behavior of birds drawn from observations of individuals that have not fully reached breeding condition.

Unfortunately for the observer, the combat activities of fiddler crabs in this phase are often more numerous and certainly more easily foreseen than are encounters between burrow holders. It is temptingly convenient to select for attention an active aggressive wanderer and watch him on his progress through the population. Such a course is usually conveniently marked by the threats of burrow holders on his route. If his aggressive phase is well established, a number of combats may be thus observed. Once the repertory of a species is partially known, of course, the combats instigated by these wanderers form a rich source of information.

The combats may be composed of one or most of the components previously described. Often, however, the high-intensity components —dactyl slides, heel-and-ridges, and interlaces— are imperfectly attained or the motions are atypical; tapping, if any, is of wide amplitude.

For example, several aggressive wanderers, after an uneventful manus rub, inserted both pollex and dactyl through the gape of the burrow holder's chela, instead of inserting only the pollex. No regular combat development by the wanderer seemed possible from this position. One such contest ended with the burrow holder's opening his chela wide and freeing himself. In another the crabs broke apart after awkward shaking and shoving. After each of these encounters the wanderer departed.

Similarly, an apparently clumsy attempt is sometimes made by the wanderer to attain a dorsal slide position. This the opponent thwarts by raising his own dactyl high. The maneuver does not happen in fully ritualized fights between burrow holders, when the opponent usually appears wholly unresisting and—one is tempted to say—cooperative. When a slide position is obtained, the wanderer sometimes saws back and forth transversely across a single spot on the opponent's upper dactyl rather than in the normal longitudinal direction.

The behavior of a burrow holder approached by an aggressive wanderer is often atypical of his normally aggressive display phase; this is true even when, as is usually the case, the wanderer is the smaller crab (Table I). As described under "Withdrawals" (p. 60), the burrow holder sometimes goes completely underground either when approached or later in the course of the encounters; sometimes he leaves the manus and chela, bent at the carpus, flat on the ground as in *maracoani* (Crane, 1958, Text-fig. 2). When the wanderer has passed, the burrow holder emerges promptly and resumes display.

All except one of the 15 forceful endings took place at the close of a burrow holder's fight with an aggressive wanderer.

2. Combats between two burrow holders— These encounters usually occur at the mouth of the burrow of one of the participants. In contrast to the usual procedure in combats started by an aggressive wanderer, the instigator in this category is usually the larger crab. A minority of encounters between burrow holders take place on or close to the boundary between two territories.

The same two neighboring crabs occasionally proceed through highly ritualized combats a number of times during a single low tide. Sometimes a burrow holder seems to be attracted to his neighbor's vicinity by a combat between the neighbor and another crab, usually an aggressive wanderer. Irregularities in the performance of the components are rare, combats brief, and forceful endings practically absent.

3. *Mutual combats*—About one-third of all combats are strongly mutual in the sense that each crab performs at least one of the ritualized components. In the 154 combats analyzed in Tables II and III, mutual elements were detected in 38% of the combats between an aggressive wanderer and a burrow holder, and in 31% of those between two burrow holders. In 87% of the mutual combats including an aggressive wanderer, the latter was smaller than the burrow holder he approached; this figure is higher than the proportion (67%) of smaller wanderers in the entire combat sample (Table I).

In a few additional combats, which are included in Tables V and VI, an aggressive wanderer's only activity appeared to be the initial approach to the burrow holder. After that the burrow holder seemed to be the sole actor and the wanderer eventually departed. Similar cases were observed twice in combats between burrow holders. No doubt many more such examples were seen than are cited in the tables; they are not included since the instigator's inactivity, whether he was a wanderer or a neighbor, could be only suspected because the angle of observation was unsatisfactory.

The heart of the problem of instigator inactivity lies in the observation of low-intensity components, the manus rubs. The actor or actors are especially difficult to detect, even in motion picture close-ups, because manus rubbing is the only component in which mutual action can be performed simultaneously by both crabs; this of course is because the necessary juxtaposition of parts—outer manus to outer manus—is much less precise than in the subsequent components of high-intensity combat. Even in the analyses of highly mutual combats the counts for mutual manus rubs are doubtless low; when uncertain about the mutuality of a rub, I counted it as absent.

In ritualized components of high intensity—dactyl slides, heel-and-ridges, and interlaces—the actors either perform the slide in turn or exchange roles, the former actor holding still while the second crab performs the next component. Any necessary shift in position is made, including those demanded by a different size of claw. Sometimes the temporarily inactive crab is not only quiescent during and after the shift but even appears to take a cooperative part in it. For example, after a slide a retiring actor brought his dactyl below that of his opponent, into the latter's gape, and then stopped moving. This left the other crab in the actor's position for the slide that promptly followed.

In mutual heteroclawed combats the heel-and-ridge is performed by the individual having his dactyl outside the manus, the interlace by the crab with the dactyl against the inner surface, as described on p. 63. When the second crab becomes the actor, he needs only to engage the claws farther, to the gape base, to attain fully the interlace position.

Only two examples of this type of heteroclawed mutuality appear in Tables V and VI, since these were the only such combats observed from their low-intensity beginnings, and for those tables it seemed best to include only fully observed examples. A total of 11 heteroclawed combats were in fact partially witnessed which included this alternate performance of heel-and-ridging with interlacing; one record was secured on motion picture film; all except one of these additional examples took place between an aggressive wanderer and a burrow holder. Other mutual components recorded in the tables were also seen in greater numbers than indicated, but again observations were partial.

Although some mutual encounters were among the best examples of ritualized combat, with no discernible trace of force, in others aggressive elements were scarcely disguised. In these combats the shift from one actor to another was clearly accompanied by irregular pushing or by abruptly jerking motions of a claw in the midst of a component.

E. Duration

A total of 104 combats of all classes, each observed from its beginning, were approximately timed, as described on p. 53. The great majority turned out to be very short encounters, most of them lasting between about 3 and 8 seconds. The duration of a few ranged from 1 to 3 minutes. No records were obtained of complete combats lasting between 20 and 60 seconds; even the addition of incompletely observed examples, however, indicated that the combats of intermediate length were rare—rarer than the few of long duration. It seem likely that when sufficient data are accumulated the curve will have two peaks.

Relevant subdivisions are given in Table VII. Of the 104 combats timed, 45 (43%) were of low intensity; all of these were short, and less than one-third included pushing with, therefore, a recognizable element of force. The others

TABLE V.

Uca rapax. MUTUAL ACTIVITY IN ENCOUNTERS BETWEEN AGGRESSIVE WANDERERS AND BURROW HOLDERS.

(Locality and dates as in Table II, p. 56. Encounters were included in this table only if they were observed from a manus rub beginning.)

Key: AW .... Aggressive wanderer
BH .... Burrow holder
AW/BH .... Activity in turn by aggressive wanderer and burrow holder

Combat Type Number	*Combat Composition*	*Total Combats Observed*	*Division of Components Between Opponents* Components	Actors			
				BH	AW/BH	AW	Identity unknown
1	Manus rub	6	Manus rub	4	2	..	..
2	Manus rub + dactyl slide	11	Manus rub	..	..	4	2
			Dactyl slide	4	2	..	..
			Manus rub + dactyl slide	5	..	..	..
3	Manus rub ± dactyl slide + heel-and-ridge ± taps	6	Manus rub	..	..	3	3
			Dactyl slide + heel-and-ridge	1	..	..	..
			Heel-and-ridge	1	..	..	..
			Heel-and-ridge with taps	4	..	..	..
4	Manus rub ± dactyl slide + interlace ± taps	4	Manus rub	1	..	1	2
			Dactyl slide	..	1	..	..
			Dactyl slide + interlace with taps	1	..	..	..
			Interlace	..	..	1	..
			Interlace with taps	2	..	..	..
5	Manus rub + dactyl slide + heel-and-ridge with taps + interlace	1	Manus rub + dactyl slide	..	1	..	..
			Heel-and-ridge with taps	1	..	..	..
			Interlace	..	..	1	..
	Total	28		24	6	10	7

TABLE VI.

Uca rapax. MUTUAL ACTIVITY IN ENCOUNTERS BETWEEN TWO BURROW HOLDERS.

(Locality and dates as in Table II, p. 56. Encounters were included in this table only if they were observed from a manus rub beginning.)

Key:
Y .... Larger burrow holder
y .... Smaller burrow holder
Y/y .... Activity in turn by larger and smaller burrow holders
Boundary .... Region approximately midway between burrows of opponents

Combat Type Number	*Combat Composition*	*Total Combats Observed*	*Place*	*Division of Components Between Opponents* Components	Actors Y	 Y/y	 y
1	Manus push	2	2 at y's burrow	Manus push	1	..	1
	+ manus rub			Manus rub	..	1	1
2	Manus rub	3	2 at Y's burrow	Manus rub	..	3	..
			1 at y's burrow		..	..	..
3	Manus rub	5	3 at y's burrow	Manus rub	..	4	..
	+ dactyl slide		2 near boundary	Dactyl slide	1	3	..
				Manus rub and dactyl slide	1	..	..
4	Manus rub	4	2 at Y's burrow	Manus rub	1	2	..
	+ heel-and-ridge		2 at y's burrow	Heel-and-ridge	..	..	1
	± taps			Heel-and-ridge with taps	1	..	1
				Manus rub + heel-and-ridge with taps	1	..	..
5	Manus rub	1	1 near boundary	Manus rub	1	..	..
	+ dactyl slide			Dactyl slide	..	1	..
	+ interlace with taps			Interlace with taps	1	..	..
6	Manus rub	1	1 at y's burrow	Manus rub	..	1	..
	+ dactyl slide			Dactyl slide	..	..	1
	+ heel-and-ridge with taps			Heel-and-ridge with taps	..	..	1
	+ interlace			Interlace	1	..	..
	Totals	16			9	16	6

TABLE VII.

U. rapax. DIVISIONS OF 104 COMBATS OF KNOWN DURATION.

Intensity	*Duration Less Than 20 Secs.*		*Duration More Than 60 Secs.*		*Total*
	With force	Fully ritualized	With force	Fully ritualized	
Low	10	35	0	0	45
High	4	46	4	5	59
Total	14	81	4	5	104

were composed of manus rubbing alone and always appeared wholly ritualized.

The remaining 59 combats (57%) each included one or more high intensity components, usually preceded by manus rubs. Eight (less than 14%) included forceful endings; about five-sixths (83%), therefore, were wholly ritualized.

As will be evident in the following sections, the figures of greatest interest are those in the duration divisions within high-intensity combat. Here 50 (85%) of the combats were of short duration, and of these 4 (8%) ended forcefully. In contrast, of the 9 (15%) long combats, 4 also ended forcefully, but the percentage (44%) was much higher.

Seven of the 9 long combats had mutual components; 3 of these 7 had forceful endings, including the eviction of a burrow holder by an aggressive wanderer. Both of the evictions in the sample came at the end of a long fight. Six of the long combats involved an aggressive wanderer, a proportion roughly in agreement with wanderers' occurrence in the combat sample. Finally, 8 (88%) of the 9 long fights were heteroclawed—a very different proportion from the 50% characteristic of the sample.

In summary, in a sample of 104 combats all but 9 lasted less than 20 seconds. Each of these 9 lasted more than a minute and contained high-intensity components. Proportionately more of these long combats occurred between right- and left-clawed crabs, more had mutual components, and more ended forcefully than did short combats.

F. Postcombat Behavior

After most encounters between *rapax* males, the opponents promptly resumed their precombat activity. Aggressive wanderers passed on through the population, instigating new combats and engaging in other activities, as already described (p. 53). Burrow holders, returning with equal completeness to all their former activities, first resumed waving.

Almost one quarter of all encounters sufficiently observed, however, were followed by detectable changes in behavior. Of all observed combats, both opponents were watched long enough in 148 examples to form a suitable basis for an examination of such changes and of combat composition when subsequent changes did not occur. These alterations in behavior were of two kinds: either the aggressiveness of an aggressive wanderer was reduced or there was an appreciable delay in the resumption of waving by a burrow holder. Reduction of aggressiveness in a wanderer and delayed waving by the burrow holder never followed the same combat, nor was waving ever delayed by both opposing burrow holders.

Table VIII breaks down the 148 combats where subsequent behavior was observed into a number of potentially relevant subdivisions. The first column, headed "Result," divides the group into those with behavior unchanged, waving delayed, or aggression reduced. In the second column, "Combat Class," the opponents' phases and relative size are indicated, as in previous tables, as well as, where necessary, the instigator and the site of the combat. Under "General Combat Composition" selected characteristics are isolated; these show the relative prevalence of low- and high-intensity combats, forceful components, tapping, and mutual components. It seemed that one or more of these aspects of combat might be correlated with behavior changes or the lack of them. However, no clear-cut correlation emerges. For example, neither tapping nor mutual components preclude either a delay in resumption of waving or reduced aggression; similarly, forceful endings are not necessarily followed by subsequent behavior changes. Nevertheless, certain trends are indicated. The information given by the table, in addition to the more limited data on combat duration (pp. 63, 66; Table VII), form the bases for the remainder of this section.

Class 1. Combats not followed by a detectable change in behavior—The 112 combats in this class comprise three-fourths of all in the sample;

TABLE VIII.

Uca rapax. BEHAVIOR OF OPPONENTS. FOLLOWING 148 COMBATS.
(Locality and dates as in Table II, p. 56.)

Key: AW .... Aggressive wanderer larger than opponent
aw .... Aggressive wanderer smaller than opponent
BH .... Burrow holder larger than opponent
bh .... Burrow holder smaller than opponent
M .... Mutual component(s) clearly present
* .... Burrow holders dispossessed; waving resumption delayed more than 2 minutes

Result	*Combat Class*	*General Combat Composition*						*Sub-total*	*Total*
		Low intensity only		High intensity					
				With forceful end		No forceful end			
		With push	No push apparent	No taps	With taps	No taps	With taps		
Subsequent behavior apparently unchanged	AW & bh	1	5 (1 M)	. .	. .	1	3 (1 M)	10	
	aw & BH	. .	15 (2 M)	5 (1 M)	. .	23 (6 M)	13 (10 M)	56	
	BH & bh (BH=trespasser)	4 (1 M)	7	. .	. .	7 (3 M)	3 (2 M)	21	
	BH & bh (bh=trespasser)	1	5 (3 M)	1	. .	4 (1 M)	5	16	
	BH & bh (on boundary)	. .	6 (2 M)	. .	. .	3	. .	9	
	Subtotals	6	38	6	. .	38	24	112	112
Resumption of waving by burrow holder delayed (less than 2 minutes except as noted)	AW & bh	. .	4	. .	2 (1 M)*	3	2	11	
	aw & BH	. .	2	. .	. .	1	. .	3	
	BH & bh (BH=trespasser)	2	3	. .	. .	2	2 (1 M)	9	
	BH & bh (bh=trespasser)	. .	. .	. .	. .	. .	. .	. .	
	BH & bh (on boundary)	. .	. .	. .	. .	1 (1 M)	2 (1 M)	3	
	Subtotals	2	9	. .	2	7	6	26	26
Wanderer's aggres-siveness reduced	AW & bh	. .	. .	2	1 (M)	. .	1 (M)	4	
	aw & BH	. .	4	. .	2	. .	. .	6	
	Subtotals	. .	4	2	3	. .	1	10	10
	Totals	8	51	8	5	45	31	148	148

61% were of high intensity. Force was detected in about 12% of all combats in the class; therefore, 88% were fully ritualized; forceful ends occurred in about 5%. Tapping was present in more than 21% of the total, never in combats where forceful ends occurred; where only high-intensity combats were counted (since tapping normally occurs only then), the percentage with tapping was 35%. Mutual components were noted in about 30%. Short combats, lasting less than 20 seconds, formed 95% of the total in a duration sample of 86 in this class.

Class 2. Combats followed by a delay in resumption of waving—Fourteen of the 26 examples in this class were between an aggressive wanderer and a burrow holder; 9 were between two burrow holders where the larger was the instigator; and 3, with the instigator questionable, occurred near a territorial boundary between burrow holders. These 26 combats form almost 18% of all combats in the sample. Waving was usually delayed by a crab at his own burrow following combat with a larger individual, either wanderer or neighbor. When a smaller crab was the instigator at the burrow of a larger crab, no postcombat waving delay occurred. Of the 26 delays, 24 lasted less than two minutes; the longer exceptions were by dispossessed crabs and are described below. The short delays included some subsequent behavior associated with combat, such as a number of the total withdrawals.

Forceful components took place in a total of 15% of the class as follows: pushing occurred in two low-intensity fights between burrow holders; two high-intensity combats, both between a large aggressive wanderer and a smaller burrow holder, resulted in eviction of the burrow holder. Because of the theoretical interest of these two fights certain combat and postcombat details are pertinent. Both included taps; one showed mutual components; neither ended in a physical upset; the duration of each was more than one minute. After the first dispossession, the wanderer descended the burrow, then emerged and began waving. Meanwhile, the former occupant assumed the low posture and moved off giving no response to the threats of neighbors. Eventually he retired down an empty burrow some six feet away, where he plugged the mouth and remained at least until the next low tide. In the second example the wanderer descended the burrow after the occupant left, emerged within a few seconds, and then abandoned it to continue his precombat behavior as a continuing aggressive wanderer. Meanwhile, the evicted burrow holder had been circling around in the low posture; as soon as the wanderer left, this crab resumed possession, descending briefly, emerging and waving promptly. The entire delay, in addition to the combat's 1.5 minutes, lasted 2.4 minutes, in contrast to the indefinite delay in waving following the first eviction.

Throughout Class 2 tapping was absent in all fights with forceful ends except in the two just described, which ended in eviction. Tapping was present in 25% of the remainder, or almost 50% of those of high intensity without force. Mutual components were absent in low-intensity combats but present in 27% of those of high intensity, including one of the evictions, and in 15% of the entire class. Short combats formed 67% of the total in a duration sample of 15.

Class 3. Combats followed by a reduction in the aggressiveness of a wanderer—Of the 90 combats between an aggressive wanderer and a burrow holder, 10 (11%) were followed by reduced aggressiveness. These 10 combats were distinguished as follows: In 40% the wanderer was the smaller crab; 60% were of high intensity and included all combats in which force was detected; these forceful endings occurred in 83% of high-intensity combats or 50% of the total in the class. Taps were included in 40% of the total, most of them in combats with forceful ends. Mutual elements appeared in 20% of the combats, all high-intensity, with and without forceful ends. Short combats formed 83% of the total in a duration sample of 6.

Comparison of combat characteristics in relation to subsequent activities—When the above classes of combat are compared, five points emerge that seem noteworthy in spite of the small samples. First, in combats followed by the reduced aggressiveness of a wanderer, forceful endings were more numerous than in combats either not followed by behavior changes or with a subsequent delay in resumption of waving. Second, long combats were most numerous in the class followed by delayed waving, less so among those resulting in reduced aggression, and rare among encounters with no detectable results. Third, mutual components were relatively fewer in combats followed by changes in behavior. Fourth, tapping was usually absent from encounters with forceful endings; this absence is probably correlated with the frequently prompt cessation of combat after tapping. When tapping did occur in the course of a fight ending forcefully, subsequent behavior was changed. Finally, after combat any changes in behavior were usually shown by the smaller crab.

Summation—because this study was made entirely in the field among unmarked crabs, few hints of summation were observed. I have in fact obtained reliable notes on the subject in only seven pairs of combats. Two of these involved examples where the actor's behavior changed following the second encounter; in each the encounter was less intensive than the first and the change consisted in reduced aggressiveness of a wanderer.

When marked crabs are adequately observed, it seems certain they will show that summation plays a part in the effects of combat.

V. COMBAT IN SPECIES OF *Uca* OTHER THAN *U. rapax*

Combat has now been filmed in fifteen species of *Uca* in addition to *U. rapax*. These species are scattered widely throughout the genus. The results are predictably inadequate, because no special effort has yet been made to record the various patterns in species other than *rapax*. As stated earlier it is only recently that the complex nature of fighting and its morphological specializations have become apparent. Hence, the lack of a filmed record of any particular component by no means precludes its existence.

Data on combat in Indo-Pacific and eastern Pacific species recorded only in field notes have been omitted from this paper. The observations were made before the importance of ritualized fighting was realized and at a period when my attention was concentrated on display. During those years all combats appeared too similar to deserve full attention, in an essentially comparative study of species, since time in the field was always limited.

Several statements can, however, now be made with relative assurance in comparing combat in other species with that in *rapax*. First, the Indo-Pacific species listed in Table IX, with the exception of three species in the old, informally

TABLE IX.

BASIC COMPONENTS OF COMBAT IN *Uca* SO FAR RECORDED ON MOTION PICTURE FILM.

(Note: Minor elements are omitted because of insufficient data. Species are arranged in systematic order, in accordance with a revision in preparation; the closest relations of *U. lactea* are American species, as indicated.)

Region	*Species (Uca)*	*Manus Push*	*Manus Rub*	*Dactyl Slide*	*Heel-and-Hollow*	*Heel-and-Ridge*	*Tapping*	*Interlace*
Indo-Pacific								
	dussumieri (Milne-Edwards)	x	x	x	..	..	..	..
	coarctata (Milne-Edwards)	x	x	..	..	..	..	..
	urvillei (Milne-Edwards)	..	x	x	x	..	Dactyl only	..
	bellator (Petiver)	x	..	..	..	..	..	..
	tetragonon (Herbst)	..	..	..	x	..	No	..
	vocans (Linnaeus)	x	x	..	x	..	No	..
	chlorophthalmus (Milne-Edwards)	..	..	..	..	x	Dactyl only	..
	inversa (Hoffman)	..	x	..	..	..	Dactyl only	..
W. Africa								
	tangeri (Eydoux)	x	x	..	..	..	..	x
America								
	maracoani (Latreille)	x	x	..	..	..	..	..
	insignis (Milne-Edwards)	x	..	..	..	..	..	..
	rapax (Smith)	x	x	x	..	x	Dactyl & pollex	x
	cumulanta Crane	x	x	x	..	x	Dactyl & pollex	x
	inaequalis Rathbun	..	x	..	..	..	..	..
Indo-Pacific								
	lactea (deHaan)	x	x	x	x	..	Dactyl & pollex	..
America								
	deichmanni Rathbun	x	..	x	..	..	..	..

named "broad-fronted group," show more tendency to forceful fighting with less ritualization. The three exceptions are *chlorophthalmus, inversa,* and *lactea.*

Second, the highly ritualized heel-and-ridges of the New World crabs are represented in some Indo-Pacific species by a lifting and gripping motion differing from that in *rapax* as follows: The pollex with its large distal or subdistal teeth either grip in or do not usually pass beyond appropriate hollows near the base of the pollex. This position is in contrast to the rubbing and tapping against the oblique ridge characteristic of *rapax, cumulanta, chlorophthalmus,* and *inversa.* The dactyl, however, holds in all a position similar to that in *rapax,* against the outer part of the manus. Only in broad-fronted *lactea* has the pollex been seen to make a series of taps in the hollow at the inner base of the pollex.

Several species typically shift from low to high intensity in a manner different from that of *rapax.* In *tangeri, maracoani, insignis,* and *inaequalis* the chela tips are turned downward, the mano-carpal joint raised, and the chelae engaged in this position, after which they swing once more to the horizontal. In all the other species in which high-intensity encounters were filmed, the chelae engaged in the horizontal position, usually at the end of a manus rub.

The variation in dactyl slides is great, as in *rapax.* Whereas the detailed study of *rapax* makes it possible to state the normal position of the dactyl during a slide, in other species the paucity of material and lack of information on individual social situations make any further statements unproductive.

VI. DISCUSSION

Two challenging aspects of fiddler combat are the obscurity of its functions and the complexity of its ritualizations. As long as the functions of fighting remain uninvestigated its ritualizations can be only superficially understood. Because of the new data presented, however, it seems timely to comment on possible functions for combat and to suggest reasons for its ritualization. The section continues with preliminary remarks on the possible origins of the components and on comparisons with combat in other animals. It closes with suggestions for further research.

A. *Functions of Combat in* Uca

A general discussion of territoriality in fiddler crabs lies beyond the scope of this paper. Here the subject will be mentioned only to the extent necessary to give a frame of reference for the consideration of combat.

In this genus the territoriality of breeding males appears to be not at all concerned with the optimum distribution of the population in respect to the food supply. Only males in the display (waving) phase, during which mating takes place, behave aggressively toward individuals in the vicinity of their occupied burrows, and then only toward males in the aggressive wandering phase or toward trespassing neighbor males. Aggressive wanderers, in contrast, neither wave, mate, nor remain near a particular burrow. The territories of the displaying crabs are not scattered equally through the population, nor are they usually to be found in food-rich locations.

Burrows of displaying crabs are often, instead, concentrated in slightly higher, drier parts of the intertidal zone, where food is less abundant. Here males in other phases are few or absent. Moreover, crabs in the display phase feed little in comparison with others, and when they do so, they often move temporarily to the richer, lower levels. Females in breeding condition in some species occupy burrows close to those of waving males; in others, receptive females move actively through the displaying portion of the population; after mating, while the eggs are developing, females usually inhabit burrows closer to the low-tide levels than those of any section of the population except the very young.

It appears rather that territoriality in *Uca* is concerned directly and indirectly with reproduction. An advantage of territories on higher ground may be that the displaying crabs are there more conspicuous. This could obviously be of importance not only in attracting receptive females but in the mutual visual stimulation of waving males. Again, the drier substrate may transmit more effectively the vibration signals of courtship. Finally, and probably importantly, territories on higher ground are uncovered by the tide for longer periods daily, thus giving more time for courtship; at least in the tropics receptive females are never abundant in any population of waving males and courting time is short at best. It must be emphasized, however, that displaying males in a given species by no means always gather into a lek-like formation; very often they are scattered, although in clear sight of one another, throughout the greater part of a population. The relative breeding success of individual males with burrows in different locations remains wholly to be investigated.

Possible explanations of fighting remain far from clear. It is unsurprising that each crab coming into territorial and display phases acquires a burrow in a spot appropriate for display and mating. But, for two reasons, there appears to be no need to obtain such a burrow through combat. First, all fiddlers of both sexes and of all ages except the very young can dig new burrows quickly and efficiently. Yet they do so only in emergencies brought on by predators or by an inrushing tide. In contrast, when a large crab evicts a small one, he enlarges the burrow suitably, with neither hesitation nor hurry. Furthermore, few areas are so crowded that there does not appear to be ample space, empty and undefended, among displaying males where new burrows could be dug.

Second, and probably more important, in all displaying populations that I have adequately observed, empty burrows are plentiful among those of displaying individuals. They have been abandoned by crabs not at the time in a burrow-holding phase; as the tide recedes, these crabs simply dig their way to the surface and go elsewhere. Yet an aggressive wanderer, unless his aggressiveness has been reduced by a fight with a burrow holder, either pays no attention to these empty burrows, or pokes into them with cheliped or ambulatories, briefly and superficially; then he moves on. These empty burrows always appear to be considerably more numerous than are the wanderers, so that no difficulty in encountering such a hole seems to be involved.

Although occasionally an aggressive wanderer stops slightly longer at a burrow occupied by a nondisplaying crab, any attempt to dig out such a crab is rare and little effort is expended. I have never knowingly seen a combat between a crab that is not in display phase and a wanderer, or between two wanderers.

In fiddler crabs no harems are maintained and single females seem never to be direct causes of intermale combat. Occasionally a male even abandons an advanced courtship, attracted by a combat between two other males.

The immediate goal of an instigator does not in fact seem to be the taking over of a suitable burrow as a center for display or a direct competition for females. Rather, the apparent aim is a combat with a displaying male.

The combat itself, as has been described in detail for *rapax,* is usually fully ritualized, with no apparent component of force; in most cases it results in no detectable change in the subsequent behavior of either crab. One or the other withdraws his claw from contact with that of his opponent; the aggressive wanderer resumes his progress through the population, threatening and entering into new combats; the burrow holder promptly resumes display, its intensity undiminished. In one such *rapax* combat in nine, however, a wanderer's aggressiveness was reduced; in one in 45, the burrow holder was dispossessed and the wanderer took over. Less intensive observation of other advanced species have yielded corroborative observations: The wanderer's behavior is similar and only rarely is there a detectable result. In those instances where a wanderer actually takes over a burrow he sometimes assumes the display phase at once; more often, he does not wave, but shortly abandons the burrow and moves on, his aggressiveness maintained and his territorial drive still in abeyance.

With these figures in mind it seems likely that combat may sometimes either advance or retard the assumption of territorial and waving phases by the wanderer. Summation, as suggested on p. 68, may well play a part here that the field techniques in use could only suggest. Combat, then, may serve as a mechanism for ensuring that suitable burrows for display are not taken over by males in subbreeding condition; nevertheless, the availability of empty burrows, noted above, forms an obvious argument against this view.

The function of combat will now be examined from the point-of-view of the burrow holder. If this displaying crab is not vigorous enough or sufficiently motivated to fend off an aggressive wanderer, he may be in an inadequate condition for breeding and should not, from the point of view of selection, be left in a position to attract receptive females. Yet many vigorous burrow holders, in other species as in *rapax,* withdraw partly or wholly from an incipient combat, even in the frequent instances where the approaching wanderer is the smaller crab; then the burrow holders resume waving and courting promptly and strongly when the wanderer has departed. The role of this withdrawal behavior in the pattern of combat remains puzzling.

After combat, however, one *rapax* in six delays waving, while one in 45 loses his burrow, with a consequent postponement of resumed display. These relative numbers agree well with impressions received in numerous more casual observations of combat in other species.

In examining the possible selective values of fighting and its ritualization a distinction should be kept in mind between these two visible results —namely reduced aggressiveness and delayed waving. Since all burrow holders are in the display phase and, as part of that phase, in a threatening and fighting mood toward both aggressive wanderers and trespassing neighbors, it seems that a postcombat reduction in aggressiveness by a wanderer normally would result only if he were not ready for territorial-display-mating behavior. In that case the "loss" of a combat would be a selective advantage. On the other hand, a reduction of display time for a burrow holder through prolonged combat would be a disadvantage.

A reasonable suggestion, therefore, appears to be that the ultimate value of combat, regardless of the role of ritualization, lies in preventing suboptimal males from wasting the breeding time of the population by attracting receptive females. This explanation does not, however, account for all the facts. It takes no account of combats, almost all fully ritualized and resulting very rarely in waving delays, between vigorous burrow holders. Again, the function of downpushes remains unexplained. Here one burrow holder, far from endeavoring to take over the burrow of his neighbor or at least to dig the occupant out and engage him in combat, simply thrusts him forcefully underground before returning to his own burrow and resuming display.

When viewed as a whole it seems that the function of combat may lie primarily in stimulating and synchronizing mating behavior. As in so many other groups of animals where such an effect is suspected, proof awaits work in endocrinology and neurophysiology.

Similarly in need of the attention of physiologists are two strong impressions that recur during fieldwork on *Uca*. One is that combat may serve to release tension in the actively courting section of the population. The other impression, particularly compelling when one is watching ritualized mutual encounters, is that combat appears often to be in progress for its own sake. The attention of a third crab is sometimes drawn to a nearby combat; he may then either interrupt or engage one of the participants after the end of the first encounter. Even more suggestive are the sequences of high ritualization discussed below.

B. The Question of Adaptive Values of Combat Ritualization

As shown in previous sections, a large majority of combats in *Uca rapax* show no detectable element of force and hence may be termed fully ritualized. More casual observations on other species indicate that ritualization is similarly prevalent throughout the genus. In searching for the selective advantages of ritualization the immediate effects of individual combats have proved unilluminating. As is well known, even the most violent fights in *Uca* practically never result in physical damage; no injury at all was ever seen in *rapax*. It seems, therefore, that a protective function, which has been considered obvious in the ritualized encounters of many well-armed animals, is not now of importance in fiddler crabs.

Again, the data in this paper on *rapax* give no evidence that ritualized encounters are any more likely than the uncommon forceful fights either to promote or to prevent behavior changes in an opponent. This is true in general both of reductions in the aggressiveness of a wanderer and of delays in resumption of waving by a burrow holder.

The only apparent advantage of ritualization in *rapax* seems, rather, to lie in the shortening of combats. The counts so far made indicate clearly that ritualized encounters are not only far more numerous than those including components of force but also that they are shorter, most lasting less than 10 seconds. In contrast, forceful fights continuing more than one minute are usual. This is true whether or not a forceful combat results in subsequent visible behavior changes for either crab. While this difference in duration appears to have no obvious importance for an aggressive wanderer, the shortening of combats through ritualization may well be a selective advantage through its effects on burrow holders.

This suggestion is based on both the ecology and the mating behavior of *Uca*. Since they court only during low tide, and are usually further restricted by other requirements, both meteorological and physiological, their periods for courtship and mating are limited. Combat and courtship cannot proceed simultaneously and, in *Uca*, the combats of males seem to hold no attraction whatever for females. Therefore it seems clear that, by shortening combats, ritualization ensures that courtship opportunities are minimally reduced.

It may be that an important factor in waving display lies in its stimulating effect on other males, or in the synchronizing of breeding activities. Here, too, a shortening of each combat would advantageously shorten the time during which one or two wavers did not contribute to the communal effect.

One characteristic of ritualized combat becomes increasingly apparent with continued observation. This consists in the leisurely, formalized, and wholly unforceful cooperation sometimes apparent between the two opponents. A highly ritualized encounter in *rapax* may run about as follows. An instigator, whether wanderer or neighbor, approaches a burrow holder. A rub by one or both crabs, outer manus against outer manus, usually follows. Next, the instigator sometimes holds perfectly still while his opponent slowly eases his chela into the actor's slide position; the two crabs may then reverse the role, the shift being accomplished slowly, without fumbling, and with the apparent cooperation of the crabs. In a few moments they may progress to a similar alternation of heel-and-ridging or, in heteroclawed encounters, to an alternation of heel-and-ridging with interlaces. In other examples a single opponent may be the actor throughout, the second crab holding himself quietly. When the actor breaks off, both crabs move apart and resume their pre-encounter activities.

Observation of these encounters gives a strong impression that they provide one or both crabs with satisfactions that are not concerned in direct goals, such as taking over a burrow or evicting a trespasser; the activity itself seems to serve as the goal. We know nothing at all yet about the means of conferring satisfaction—whether through the performance of the motions, or through the reception of associated sensory stimuli.

If ritualization does indeed operate selectively through shortening combats and thus providing more time for courtship, then an obvious pressure would be toward even shorter ritualized encounters. Ultimately the action might be reduced to a token touch of mani or single rubs of ridges by briefly overlapping chelae.

This trend is not apparent. According to our present knowledge, the socially advanced species have the largest repertoire of combat actions and the most extensive structural specializations for high-intensity encounters. If ritualization shortens combats, then further elaboration could nullify the effect. Occasional prolonged encounters in *rapax,* fully ritualized and elaborately mutual, suggest that this process may prove to be a factor in current evolution.

C. Derivation of Components

Too little comparative work has yet been done to discuss the comparative ethology of combat in *Uca.* Nevertheless it seems worthwhile to suggest two basic derivations that may be kept usefully in mind during future studies.

It seems likely that high- and low-intensity components have been derived from different sources. These are, respectively, from forceful fighting itself and from the fronto-lateral threat gesture common to most crabs. If the direction of evolution has been, as seems apparent, the reduction of forceful combat through ritualization, one logical point for the application of a deterrent would be immediately before the grip. The high-intensity components all appear to have originated directly from unritualized forceful grips. All take place with the two claws partly or wholly in a position for grasping each other; when, rarely, a ritualized encounter proceeds to a grip, little or no change in basic claw position is made. Unsurprisingly, specializations appear to have been added one in front of another, the interlace of *rapax* being perhaps the closest now known to the original fighting grip. The ultimate ritualization, then, would be logically the low-intensity manus rub.

However, the manus rub seems most credibly to have evolved from the warding-off lateral threat gesture, which is almost universally present in crabs. But threat gestures in many animals are themselves certainly to be understood as ritualizations of fighting, where a weapon, impressive size, or other potential advantage is exhibited, usually with exaggeration or embellishment. By these criteria, the threat gestures of crabs, including *Uca,* qualify as ritualized fighting. It seems that in *Uca,* however, manus rubbing is a further ritualization derived from a basic threat posture.

D. Comparisons with Ritualized Combat in Other Animals

The ritualizations of combat through threat displays are of course endlessly varied among animals, perhaps culminating in the displays of sound, color, and movement in many territorial birds. In fiddler crabs parallels are close.

In encounters where two individuals come actually into contact, however, comparisons are far less satisfactory. Checked point by point with *Uca* combat, the harmless poking and heaving of fighting beetles or the ritual butting and kicking of ungulates are simple, coarse, and slow while the associated structures seem relatively unspecialized. A search of the literature has not yet yielded, even among deer, an apt comparison. It seems that no buck rubs a certain antler prong gently against a different prong, suitably shaped, on his opponent's armature, then holds still while the other gets into position and rubs in turn and, finally, passes on to a further step in the sequence. Schaller's (1967) detailed comparative study of combat in eight Indian ungulates indicates no such refinements. There seems to be in fact not even a rough analogy to perhaps the highest *Uca* specialization of all, where adaptations exist even to the different requirements of opponents with the ritualized weapon on the same or opposite sides of their bodies. In other decapod crustaceans it seems certain that many spines and ridges, that have been as in *Uca* of purely taxonomic interest, will prove to be as functional as in fiddlers, and perhaps in similar fashion.

E. Areas for Further Research

The following aspects of *Uca* combat particularly need attention before the wider implications of the subject can be investigated.

1. Sensory aspects—It is not yet known whether the rubs and taps of combat are perceived by the crabs and, if so, which senses are involved. Acoustic elements will probably prove to be part of the pattern of fiddler combat as in their other types of social behavior; I have heard rasps and clicks during examples of each of the components. It seems likely, however, that tactile sensations are also important. For that reason the term "stridulation" has not been used in this contribution.

2. Neurophysiological and hormonal aspects of phase and of behavioral changes following combat—These basic problems are more than ready for investigation. They should be undertaken in a laboratory adjacent to wild populations, or at least in one equipped with a large crabbery. This specialized terrarium should include provisions for artificial tides; for controlled salinity, temperature, and light; for a substrate natural for the species, changed at suitable intervals; and for frequent restocking. In short, adequate results could not be obtained from fiddlers in finger bowls.

3. Duration of individual combats—The data in the present paper on the timing of combats are particularly inadequate in view of the tentative conclusion that the primary function of ritualization in *rapax* is the shortening of combat. In future work on all species, the behavior associated with combat should certainly also be timed.

4. Combat at night and underground—The occurrence and form of encounters at night and in burrows need examination. The deep pits at the pollex base that in some Indo-Pacific forms apparently serve as "brakes," and are often marked by puncture wounds, are represented in *rapax* and its relations respectively by slight depressions and faint scratches. No gripping has ever been seen in *rapax* in this position; perhaps such a grip is used only when an intruder enters an occupied burrow. Observation burrows can be devised in the laboratory.

5. Mathematical analysis—The distinctness of components in most combats at first glance makes a mathematical approach to combat analysis seem feasible and attractive. But success in such undertakings is endangered by a number of pitfalls. Quantitative analysis could be misleading unless based on accurate, detailed knowledge of the full combat repertory and its related behavior in the selected species, and on influences of seasonal and other rhythms. The principal threats to the significance of conclusions include: the difficulty of observing the exact beginnings of combats; the partial distinctions between homoclawed and heteroclawed encounters; the existence of mutuality and the difficulties in distinguishing it; the hard-to-gauge degree of basic aggressiveness in contrast to the cooperation sometimes apparent; the need for definite establishment of the phases of the opponents; the frequent irregularities in combats involving aggressive wanderers; and the difficulty of assessing the effects of summation.

6. Marked crabs in a fenced wild population—Many of the difficulties listed could be reduced by fencing a suitable intertidal area, large enough to give wanderers space to move about normally.

7. Comparative ethology — Contrary to my earlier conclusions, it is now clear that interspecific distinctions in combat behavior are numerous enough to make their comparative study highly rewarding. While the differences are not nearly as striking as in display there is no question but that they both illumine evolutionary trends in species groups and show most interesting steps in the development of combat ritualization.

8. Instigation and frequency of combat—The conditions leading to combat between individuals and controlling its frequency in a population deserve the closest attention. Most of the following factors, all virtually uninvestigated, will probably prove pertinent: precombat threat behavior, length of time since phase of each opponent began, age, individual variation, semilunar and other rhythms, population density, and infra-specific differences.

VII. Summary

This contribution concerns a field study of combat between male fiddler crabs. Except for preliminary comparisons with a few other species, the report is based on several hundred combats observed in a population of *Uca rapax* (Smith) in Trinidad. Descriptions of the various aspects of the subject were derived from between 104 and 180 examples watched or photographed in sufficient detail for each purpose.

The combat pattern in *rapax* shows seven distinct components, five of them highly ritualized and each of the five associated with particular morphological specializations. The frequency of three of the components is related to the juxtaposition of the large claws: when one crab has the claw of the right side enlarged and his opponent that of the left, the components tend to be different from those observed when both crabs have the large claw on the same side. Most combats last only a few seconds and infrequently include the unritualized components of force; when they do so, the fights are often longer and may last several minutes. Two or more ritualized elements, usually performed in a fixed sequence,

compose most encounters. In each component one crab rubs and sometimes taps with teeth on his own claw a tuberculated ridge or other particular structure on the claw of his opponent. Many combats are mutual in the sense that each crab performs at least one of the components; sometimes the same component is performed by each crab in turn. The sensory aspects of ritualized combat have not yet been investigated.

Combats divide sharply into two categories. The first takes place between an aggressive wanderer and a burrow holder in the display phase; its components are often irregular; practically all combats ending in forceful grips and upsets belong in this category. In the second, the opponents are two neighboring burrow holders; irregularities and force are both uncommon. The relative size of the opponents is a factor in the development of combats and in various associated activities.

The great majority of combats, whether wholly ritualized or not, result in no detectable change in the behavior of either crab. Each opponent continues either to wander aggressively or to wave beside his own burrow. Only twice, both after long fights, was a burrow holder dispossessed by an aggressive wanderer with an associated indefinite delay in further waving and, therefore, courting activity. One combat in nine results in a reduction of aggressiveness by the wanderer; one in six is followed by a very short delay in waving resumption by a burrow holder. Combat does not appear to be concerned, even indirectly, with the food supply; it neither involves nor attracts females; it appears to be unnecessary for the securing of suitable burrows as display centers and mating sites.

It is suggested, therefore, that the functions of combat must be sought in indirect physiological needs connected with reproduction, such as stimulation or the release of tension. It is further suggested that the principal selective advantage of ritualization lies not in the prevention of physical injury or of loss of display phase but rather in the shortening of combats. In this way less of the brief time suitable for courtship is lost in fighting.

VIII. REFERENCES

ALTEVOGT, R.

1957a. Untersuchungen zur Biologie, Ökologie und Physiologie Indischer Winkerkrabben. Zeit. Morph. u. Ökol. Tiere 46: 1-110.

1957b. Beiträge zur Biologie und Ethologie von *Dotilla blanfordi* Alcock und *Dotilla myctiroides* (Milne-Edwards) (Crustacea Decapoda). Zeit. Morph. u. Ökol. Tiere 46: 369-388.

1962. Akustische Epiphanomene im Sozialverhalten von *Uca tangeri* in Sudspanien. Verhand. Deutsch. Zool. Ges. 22: 309-315.

1964. Ein antiphoner Klopfkode und eine neue Winkfunktion bei *Uca tangeri*. Sonder. Zeit. Naturwiss. 24: 644-645.

BAERENDS, G. P.

1950. Specializations in organs and movements with a releasing function. Symp. Soc. Exp. Biol. 4: 337-361.

BEER, C. G.

1959. Notes on the behaviour of two estuarine crab species. Trans. Roy. Soc. N. Z. 36: 197-203.

BLEST, A. D.

1961. The concept of ritualisation. *In* W. H. Thorpe and O. L. Zangwill (Eds.), Current problems in animal behaviour. Cambridge University Press, London and New York. 424 pp.

BOVBJERB, R. V.

1960. Behavioral ecology of the crab, *Pachygrapsus crassipes*. Ecology 41: 668-672.

CRANE, J.

1957. Basic patterns of display in fiddler crabs (Ocypodidae, Genus *Uca*). Zoologica 42: 69-82.

1958. Aspects of social behavior in fiddler crabs with special reference to *Uca maracoani* (Latreille). Zoologica 43: 113-130.

1966. Combat, display and ritualization in fiddler crabs (Ocypodidae, Genus *Uca*). *In* A discussion on ritualization of behavior in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B. No. 772; Vol. 251: 213-226.

DEMBOWSKI, J.

1925. On the "speech" of the fiddler crab, *Uca pugilator*. Travaux Inst. Nencki 3: 1-7.

GUINOT-DUMORTIER, D. & B. DUMORTIER

1960. La stridulation chez les crabes. Crustaceana 1: 117-155.

HAGEN, H. O. v.

1962. Freilandstudien zur sexual-und-Fortpflanzungsbiologie von *Uca tangeri* in Andalusien. Zeit. Morph. u. Ökol. Tiere 51: 611-725.

HIATT, R. W.

1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Science 2: 135-213.

HINDE, R. A.

1966. Animal behavior. McGraw-Hill Book Company, New York. 534 pp.

HUXLEY, J. S.

1914. The courtship-habits of the great crested grebe (*Podiceps cristatus*) with an addition to the theory of sexual selection. Proc. Zool. Soc. Lond. p. 491.

1966. Introduction. *In* A discussion on ritualization of behaviour in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B. No. 772; Vol. 251: 249-271.

HUXLEY, J. S. *et al.*

1966. A discussion on ritualization of behaviour in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B. No. 772; Vol. 251: 247-526.

LORENZ, K. Z.

1941. Vergleichende Bewegnugstudien an Antinen. J. für Ornithol. 83: 137-213, 289-413.

1964. Ritualized fighting. *In* J. D. Carthy and F. J. Ebling (Eds.), The natural history of aggression. Academic Press, London and New York. 39-50.

1966a. On aggression. (Trans. by Marjorie Kerr Wilson.) Harcourt, Brace & World, New York. 306 pp. (Originally published, 1963, under the title Das Sogenannte Böse. Borotha-Schoeler, Vienna.)

1966b. Evolution of ritualization in the biological and cultural spheres. *In* A discussion on ritualization of behaviour in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B. No. 772; Vol. 251: 273-284.

PEARSE, A. S.

1912. The habits of fiddler-crabs. Philippine J. Sc. D, 7: 113-133.

REESE, E. S.

1964. Ethology and marine zoology. Oceanogr. Mar. Biol. Ann. Rev. 455-488.

SALMON, M.

1965. Waving display and sound production in the courtship behavior of *Uca pugilator*, with comparisons to *U. minax* and *U. pugnax*. Zoologica 50: 123-149.

SALMON, M. & J. F. STOUT

1962. Sexual discrimination and sound production in *Uca pugilator* Bosc. Zoologica 47: 15-19.

SCHALLER, G. B.

1967. The deer and the tiger: a study of wildlife in India. University of Chicago Press, Chicago. 370 pp.

SCHÖNE H. & H. SCHÖNE

1963. Balz und andere Verhaltensweisen der Mangrovekrabbe *Goniopsis cruentata* Latr. und das Winkverhalten der eulitoralen Brachyuren. Zeit. für Tierpsychologie 20: 641-656.

THORPE, W. H.

1966. Ritualization in ontogeny. I. Animal play. *In* A discussion on ritualization of behaviour in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B. No. 772; Vol. 251: 311-319.

TINBERGEN, N.

1952. "Derived" activities; their causation, biological significance, origin and emancipation during evolution. Quart. Rev. Biol. 27: 1-32.

1953. Social behaviour in animals. Methuen and Co., Ltd., London. 150 pp.

TWEEDIE, M. W. F.

1954. Notes on grapsoid crabs from the Raffles Museum Nos. 3, 4 and 5. Bull. Raffles Mus. Singapore (25): 118-127.

VERWEY, J.

1930. Einiges über die Biologie ost-indischer Mangrovekrabben. Treubia 12: 169-261.

EXPLANATION OF THE PLATE

PLATE I

Combat in *Uca rapax* (from 16-mm. motion picture film). See text, pp. 57—59.

FIG. 1. Tap following a heel-and-ridge in homoclawed combat. The actor is the crab on the right. His dactyl is striking the heel of his opponent's manus while his pollex is free.

FIG. 2. Same combat as in Fig. 1. Alternate stroke showing the actor's pollex against his opponent's invisible oblique ridge, on inner side of manus.

FIG. 3. Interlace in a heteroclawed combat. The actor is on the right. The teeth near his dactyl's base are starting to rub downward against the ridges of his opponent's inner manus, which parallel the dactyl's base.

FIG. 4. Same, near end of downward stroke of rub.